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FOOD-PLANT OF *JACKSONIA PAPILLATA* THEOBALD (HEMIPTERA : APHIDIDAE.)

By Miss D. J. Jackson, F.R.E.S.

Mr. Stroyan in his recent paper (1950) casts doubt on my food-plant record for this species, as quoted by Mr. Theobald (1923, 1926), and, in support of his view, he refers to Mr. Theobald's record of my finding *Hyalopteroides pallida* Theobald, now known to be a graminivorous species, on potato. In my diary for 1922, the year in which I took both species at Swordale, Evanton, Ross-shire, I have found entries which throw light on both captures. On 28th June I noted the finding of a single specimen of a green aphis crawling on the leaves of potato growing on a rubbish heap. I sent this specimen to Mr. Theobald in November, 1922, and in his letter of 24th November, 1922, he wrote of it, " The interesting thing is a single apterous female taken at Swordale on potato leaves. This is *Hyalopteroides pallida* Theo., of which the only specimen known comes from an ants' nest." Mr. Theobald obviously attached no biological significance to this record, as, in his book, he makes no claim to potato being the food-plant of this species. In the light of subsequent knowledge there is little doubt that the specimen had wandered from grass weeds, growing on the rubbish heap, on to the potato.

As regards *Jacksonia papillata*, the circumstances are rather different. On 23rd August, in a garden at Swordale, I collected aphids from one or two sickly plants of potato left in the ground after the rest of the row had been lifted. On the leaves of one plant a very small brownish ochreous species was found, one slide of which was submitted to Mr. Theobald. In his letter of 24th November he stated that they belonged to a new genus, near *Myzus*, which he was calling *Jacksonia*. This slide is now in the Theobald Collection at the British Museum, and Dr. W. E. China, who has kindly examined it at my request, informs me that it contains 1 adult female and 4 nymphs of varying instars. Another slide is in my collection, labelled in my handwriting "*Jacksonia papillata* Theo., Brownish ochreous, on potato leaves, Swordale 23-8-22." This slide (which has now been seen by Mr. Stroyan) contains 2 adult apterous females and 4 young in different instars. All these specimens were certainly found upon potato leaves in the circumstances described, but it may be suggested that they had been feeding on grass weeds (if such were present) before the ground was disturbed by potato lifting. The evidence now available, which Mr. Stroyan has kindly supplied to me, certainly shows that grass is well authenticated as a food-plant of this species. It is interesting to find that Dr. Wood-Baker (1950) has observed that the colonies of *J. papillata* were always small, containing usually only 6 to 12 individuals, and that this aphid grows very slowly, even under summer conditions, producing its young singly at rather long intervals. This would suggest that the colony I found on potato had been established on the leaves for some time. He also notes that this aphid was to be found in positions (under stones, etc.) where the grass was etiolated, and Mr. Stroyan found the apterae feeding on the colourless basal portion of grass stems. Further investigation may yet corroborate my evidence, and prove that the species feeds also on potato, with, possibly, a preference for etiolated leaves.

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POSTSCRIPT.

By H. L. G. STROYAN, M.A.

Miss Jackson has kindly given me an opportunity to read her account of the original capture of *Jacksonia papillata* Theobald before publication. I very much regret that owing to careless writing the sentences in my paper to which Miss Jackson refers appear to impugn the factual accuracy of her observations. The intention was not to cast aspersions on the genuineness of these observations ; in view of the known propensities of aphids for wandering on to abnormal food-plants at times of adversity on their true hosts, there can of course be no grounds, nor is there any necessity, to question the exactness of the recorded observations.

The doubts expressed in my remarks are in fact doubts as to whether the presence of *Jacksonia* on potato can now be regarded as biologically significant, in view of considerable recent evidence which indicates grasses as the true hosts of the genus. Senescent foliage would appear to have a strong non-specific attraction for aphids on account of its high content of mobilized nitrogenous compounds, and this may perhaps also be linked with Miss Jackson's own reference to etiolated parts, where a similar state of very active translocation connected with rapid elongation of the etiolated shoots probably occurs.

My reference to the occurrence of *Hyalopteroides* also on potato was included on the basis of a supposition that the same local conditions which could bring such a truely graminivorous aphid on to potato foliage might also have been responsible for the presence of *Jacksonia* on potato ; however, I now understand from Miss Jackson that the two occurrences were not either contemporaneous or in the same locality at Swordale, so this assumption, while still a possibility, cannot be given any weight in the discussion.

I hope that this additional note will serve to correct the unfortunate ambiguity in my original account ; and I offer my apologies to Miss Jackson for any annoyance caused to her by the imperfect expression of my arguments.

ON THE BIOLOGY OF SOME BRITISH COCCOIDEA

By Dr. K. L. Boratynski.

(*Dept. of Entomology, Imperial College of Science and Technology.*)

It is generally believed that " the indigenous British Coccids are univoltine . . . (a rule that) . . . does not apply to tropical forms and to species living under glass " (1). Recent (1948–1949) observations on the Coccid fauna at the Imperial College of Science and Technology Field Station, Silwood Park, nr. Ascot, Berks, revealed that among 30 species known to occur there, three (*Pseudococcus paludinus* Green, *Eriococcus* sp., and *Matsucoccus pini* Green) regularly have two well-separated generations in the year.

The young larvae of *Pseudococcus paludinus* (host plants: *Veronica chamaedrys* and *Achillea millefolium*, occasionally *Viola* sp., *Lotus corniculatus* and *Chrysanthemum* sp.), appear in April, and in about ten weeks develop into adults (first generation). The eggs deposited by the females at the end of June hatch in three to four weeks; the young larvae are found in the middle of July, and the adults of the second generation are mature by the end of September. The eggs now deposited overwinter and hatch the next spring in April. Males occur, but probably because both puparia and adults are very inconspicuous, only a few have been discovered.

Eriococcus sp. (host plants: *Achillea millefolium* and *Veronica chamaedrys*) is apparently new and will be described elsewhere. It is distinct from any of the known British species and related to *E. bahiae* Ehrh. (2), but differs from it in several important characters. It occurs together with *Ps. paludinus* and the life-cycles as well as some habits (e.g., feeding, selection of sites for oviposition and pupation, overwintering, etc.) of both species are remarkably similar. The young larvae of both appear simultaneously in April, but the time required for complete development of *Eriococcus* is somewhat shorter, the adults maturing earlier, seven to ten days in the summer, three to four weeks in the autumn before *Pseudococcus paludinus*. The ratio of males to females is about 1 : 1 in both generations. The eggs of both species collected in autumn and kept in tubes under ordinary laboratory conditions hatched in January, a fact possibly suggesting that the insects may be potentially multivoltine.

Matsucoccus pini (host plant: *Pinus sylvestris*), hitherto known only from a few specimens of adult females from Oxshott (3, 4), proved to be abundant in several localities in Southern England. An inconspicuous species, it remains stationary for most of its life concealed under the bark " plates"; the mobile stages (young larvae and adult females) are active for a short time (usually several hours only) after emergence. The species overwinters in the immature stages. The first generation of females appears in the middle of May and in a few days completes oviposition. The young hexapodous larvae hatch in the middle of June, settle, grow considerably, and moult into the apodous intermediate form from which the second generation of females emerges in August–September. The eggs now deposited hatch in two to three weeks, and the hexapodous larvae are found at the end of September to early October. They settle, overwinter as more or less fully developed first-stage larvae, and complete their development by the middle of the following May, when the females emerge. No males have been found in the field, and rearing experiments indicate that the species is parthenogenetic. At present 17 species (5, 6, 7, 8), all from various species of pine, are referred to this interesting genus. Of these, the life-histories of five or six (among them *M. feytaudi* Ducasse from S.W. France) have been studied and found to be univoltine. A few N. American species are recognized as serious pests of pines. Our species occurs chiefly on the lower branches of old pines, and on young trees growing in adverse conditions. In a few cases, young trees which died in such overcrowded and shaded situations showed signs of very heavy infestation.

In 1916, E. E. Green (9) suggested a possible second brood in the year of *Eriopeltis festucae* Fonsc. Some observations at Silwood Park seem to support this suggestion, but the collected data as a whole are somewhat confusing and further study is required.

The excellent facilities provided by the Imperial College Field Station have made the detailed observations on Coccids possible, and comparatively easy. I am very grateful to Professor J. W. Munro for the opportunity to work there and for his interest in my work.

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THE ABILITY OF ADULT GRASSHOPPERS TO CHANGE COLOUR ON BURNT GROUND.

By E. Burtt, D.Sc., D.I.C., F.R.E.S.

Introduction.

Poulton (1926) records that many African Orthoptera and some other insects are to some degree melanic when occurring on burnt ground, and gives evidence that certain Acrididae possess the power of adjusting their colours to the tints of their surroundings. Commenting on material collected by the late Mr. C. F. M. Swynnerton from recently burned areas in Southern Rhodesia in 1913, he remarked, " Since the grass had been burnt recently—probably not more than three or four days—the response to stimulus must be very rapid. Direct experimental evidence is much to be desired . . . ." Burr (1928–29) recorded his field observations on this point made in Angola and I made similar observations in Tanganyika, noting that melanic individuals occurred disseminated *widely* over areas which had recently been burnt, and that with regard to burnt areas generally the degree of melanism manifested varied in different species. At the same time specimens of the same species occurring well within areas of dry unburnt grass were not melanic. *Aulacobothrus wernerianus* (Karny) affords a good example. Adults from dry-grass localities have rather slate-grey markings on a pale buff coloured general background. There is a prominent pale longitudinal streak on the pronotum, with light-coloured lines on either side of it ; these two lines together form a mark shaped somewhat like a letter X. Examples of this pale form are shown in Plate 1, figs. 1–4. Those from burnt ground have the markings deep black and the background is also heavily infuscated. This applies also to the longitudinal streak on the pronotum, but the X-shaped markings usually still remain light and conspicuous. Examples are shown in Plate 1, figs. 5–8. Between June and November, 1947, I carried out some simple tests to investigate the relationship between these two colour forms.

The experimental observations were made at Old Shinyanga, some ninety miles south of Lake Victoria on the western part of the Central Plateau of Tanganyika Territory at approximately 3800 ft. above sea level. The climate there, as over most of East Africa, is semi-arid. Rainfall averages about 30 inches in the year, and most of this falls from December to May. There is no effective rain during the ensuing six months. The herbage dries out from May onwards, and the greater part of the area, if left unprotected, becomes swept by grass fires. Round Shinyanga these fires usually start in July, and considerable expanses of country are left charred and blackened.

The majority of Acrididae breed only during the rainy season, the new generation of adults appearing from late March to early June. This applies to the two species concerned in this paper, *Aulacobothrus wernerianus* (Karny) and *Tylotropidius speciosus* (Walker). My experience of Acrididae at Shinyanga, and in other areas which have a severe dry-season climate, forces me to believe that the majority of species aestivate as adults in a dormant state partially, or totally, at this period of the year, only to reappear suddenly when the rains break. *A. wernerianus* does not behave in this way, but remains active throughout the dry season and occurs abundantly in suitable localities.

TESTS ON BURNT GROUND.

Half a mile north of Old Shinyanga there is an air landing-strip where the grass is kept short. It remained unburnt during the period my tests were made. *A. wernerianus* of the pale colour form shown in Plate 1, figs. 1–4, occurred there abundantly. They did not alter appreciably in appearance throughout the dry season. A typical example taken on 21.xi.47 is shown in Plate 1, fig. 11. A few *T. speciosus* also occurred there. The material which I used for the colour-change investigation was all obtained from this locality.

At the beginning of the dry season, on 18.vi.47, the new generation of adult *A. wernerianus* having recently appeared, a batch "A" of non-teneral living specimens was collected. Some were killed and mounted. They had the appearance as shown in Plate 1, figs. 1–4. Twenty others were housed in a wooden box (dimensions 2 × 1½ × 1 ft.), to which copper mosquito-gauze had been fitted front and back. They fed readily on young millet shoots, and were kept in a room where direct sunlight could not reach them. On the same date two males and two females were chosen at random also from batch "A," and placed in a similar container outside in direct sunlight on a small patch of about four square yards of freshly burnt grass (Test 1). The box was so placed that the gauze at the back rested on the burnt ground and the other gauze face was directed upwards. Thus the contained insects were subjected to strong sunlight. A few handfuls of charred grass and ashes were sprinkled inside and a shoot of green millet added as food. After only two days both females had darkened noticeably in colour whereas the males had not. All four were killed and mounted on the fourth day. A male and a female from this first test are shown in Plate 1, figs. 9 and 10. The specimens on green millet indoors had not changed. These were kept alive as controls also for Test 2, which was begun on 25.vi.47. A batch of 120 non-teneral specimens was collected from the air-strip. A few were mounted, and the remaining 110 were placed in a larger cage (4½ft square × 3 ft. high) having wire gauze top and sides supported on a wooden framework, but open to the ground at the bottom. On this occasion the cage was placed on another small patch of freshly burnt ground measuring about four yards square and exposed to direct sunlight as before. There was heavy mortality among the grasshoppers through their being devoured by ants. As in Test 1, some had deepened noticeably in colour by the second day. After four days the 14 survivors were killed and mounted. Four males and five females had become melanized; examples are shown in Plate 1, figs. 12 and 13. Two males and three females exhibited practically no change. Meanwhile those of batch "A" on green millet leaves in the shade had not altered. On 15.vii.47 a similar test (Test 3) was made using 160 non-teneral specimens from the air-strip. The 26 survivors were killed and mounted on the seventh day. Five of the males had darkened appreciably, but two had not. Twelve females had become fairly heavily melanized while in eight the colour remained unaltered.

The adults which had melanized in the course of the foregoing tests were all ones which had emerged comparatively recently. The effect on 5-months-old adults was examined on 18.xi.47 (Test 4) in the same manner as described for Tests 2 and 3, save that now the cage was placed on a more extensive patch of ground (15 × 40 yards), which had been burnt more than three months previously. Only five of the 120 *A. wernerianus* survived by the sixth day. All (2 males and 3 females) had become deeply melanized. Examples are shown in Plate 1, figs. 14 and 15, with number 11 serving as control to this test.

SUBSIDIARY TESTS.

On 4.vii.47 60 living specimens from the air-strip were kept in complete darkness in a closed box having charred grass and ashes on its floor, together with a few shoots of green millet. Mortality was heavy, but two examples survived to the twelth day. Neither these nor the ones which had died showed any indication of colour change. This test was repeated with 80 specimens on 29.vii.47, but all had died by the eighth day, no change having taken place.

On 2.vii.47 20 non-teneral specimens from the air-strip were kept in shade on green millet shoots in a small cage similar to that used in Test 1, but having the woodwork inside painted black. Eleven survived after ten days, without manifesting change. On 12.vii.47 this blackened cage was placed outside in direct sunlight amid grass for eight days. However, considerable protection from the sun was afforded by the wooden top of the cage. No change in colour occurred. Seven now survived, so charred grass and ash was scatttered on the bottom of the cage and the latter kept in shade indoors for a week. Still there was no change in colour. Only three survived by this time. The cage was transferred to a patch of burnt ground in direct sunlight outside, but the experiment was terminated abruptly on the second day—all being destroyed by ants.

TESTS WITH ANOTHER SPECIES ON BURNT GROUND.

A few analogous tests were made with *Tylotropidius speciosus*. Several taken on the air-strip were mounted as controls. All were normally pigmented, having a pattern of dark brown on a lighter brown background. A single male was placed outside in the cage on burnt ground on 1.viii.47. By the seventh day it had become heavily infuscated. Three females and two males were included with Test 4 on 18.xi.47. By the sixth day both the males and two of the females had become melanized, but the remaining female had darkened only slightly after 11 days.

SUMMARY.

It has been shown that the *adult, non-teneral* Acridids, whether recently emerged or several months in age, can change in appearance and become melanized when kept on burnt ground. This change occurs rapidly, being

sometimes noticeable after as little as two days. The change can take place on freshly burnt ground, or on ground burnt some months previously. The area of burnt ground need only be very small if the insect is confined to it. All the specimens in which the change occurred were subjected to direct, intense sunlight, which may be an essential factor. A proportion of those tested did not change colour during the brief periods of observation; it is possible such failures are more frequent in the early dry season, when conditions are cooler, than in the late dry season, when radiation is intense. The question as to whether the reverse change could take place—that is whether melanized grsshoppers lose their black markings again if transferred to a suitable environment—was not subjected to experiment. Field observation indicates to the contrary, since heavily melanized individuals may occur in burnt areas up to several weeks after the latter have flushed with young green grass following the onset of the rains.

The principle which has thus been demonstrated to apply to two very dissimilar species seems likely to apply to melanized ACRIDIDAE generally. It supplies further evidence in favour of the view that the pigmentation of adult Acridids may be subject to striking changes (Burtt and Uvarov, 1944), because " the integuments of many insects remain alive " (Wigglesworth, 1948).

ACKNOWLEDGMENTS.

I am indebted to Dr. B. P. Uvarov, C.M.G., F.R.S., for the interest he has shown in this matter, as well as for the help, advice and encouragement he has given me, and also to Mr. F. C. Padley of the Zoological Department of the University of Reading for photographing the specimens.

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PLATE 1.

Aulacobothrus wernerianus (Karny) showing ordinary and melanized forms (natural size).

FIGS.

1– 4.—Recently emerged, from a dry grassy unburnt locality.

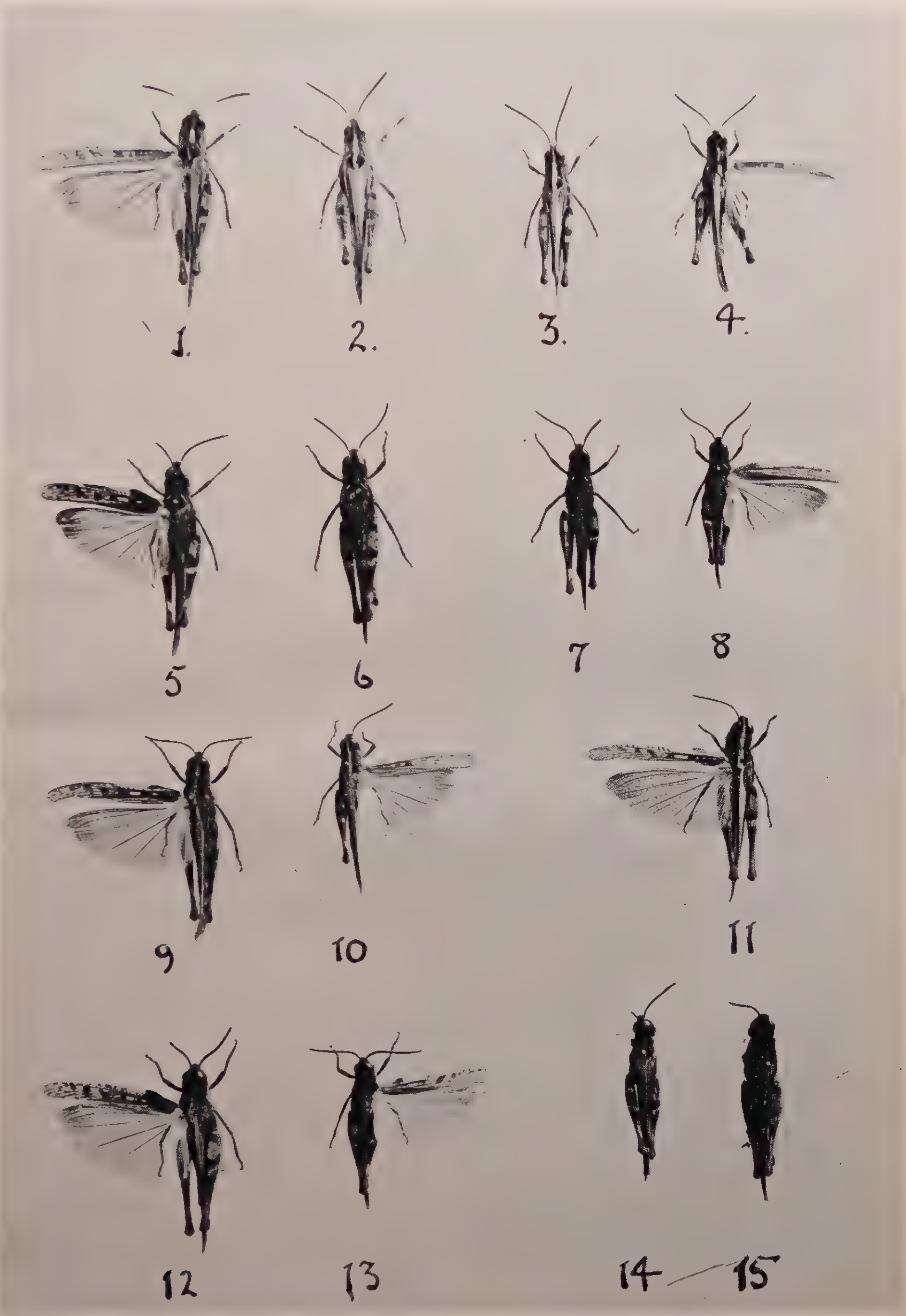
5– 8.—Melanized specimens, from a burnt area.

9–10.—Examples from Test No 1. The female (9) had darkened noticeably after two days on burnt ground. The male (10) had not changed.

11.—Five-month-old specimen from a dry grassy unburnt locality

12–13.—Examples from Test No. 2. Both sexes had become melanized by the fourth day on burnt ground.

14–15.—Examples from Test No. 4. Five-month-old specimen which had changed from the condition shown in fig. 11 after maintainance on burnt ground.



A. wernerianus showing ordinary and melanized forms.

E. Burtt.
Adlard & Son, Ltd., Dorking.

THE FACTORS WHICH PROMOTE AND INFLUENCE THE OVIPOSITION OF *NEMERITIS CANESCENS* GRAV. (ICHNEUMONIDAE, OPHIONINAE).

By J. R. Williams, B.Sc., D.I.C., F.R.E.S.
(*Entomologist, Department of Agriculture, Mauritius.*)*

I. Introduction.

The chief stimuli which attract *Nemeritis canescens* to its host and result in oviposition are comparatively well known. The present work, which makes no claim to be exhaustive, is an attempt to clarify the roles of these stimuli, and of other influences, in the complex which is responsible for this predetermined behaviour of the parasite towards its host.

The factors which regulate the behaviour of any parasitic insect towards its host may be divided into three categories—stimulatory, mechanical, and those which are influential via metabolism in the broader sense. Into the first group fall the stimuli associated with the host, which by their co-ordinated effect upon the parasite's sensory organs are conducive to oviposition. The response to such stimuli is germinally fixed, although the inherent response may be supplemented by a conditioning process during development (Thorpe and Jones, 1937; Thorpe, 1938). It is these stimulatory factors which are chiefly considered in the present work. Mechanical factors are those which play no *direct* role in the behaviour of a parasite towards its host, but which are often of considerable importance in that they either hinder or aid oviposition, which in turn may influence the parasite's response to stimulatory factors. The factors which influence metabolism need little comment; food, temperature, etc., regulate general activity, so that sense physiology cannot be completely dissociated from environment if a true picture of behaviour is to be formulated.

II. Material.

The most common host of *N. canescens* is the Mediterranean Flour Moth, *Ephestia kühniella* Zeller (Lep., Phycitidae), which was used in all experiments. For the abundant literature on the biology of *E. kühniella* reference is made to the bibliography of a paper by Richards and Thompson (1932). The moth is found in warehouses and similar places where its food, usually flour, is to be found. Eggs are laid on the flour, and the greater part of larval life is spent within silk-lined burrows in the food material. These burrows are concentrated in the top few inches of the flour. When the caterpillars are fully grown they often leave their food material and migrate upwards if possible. This wandering stage lasts for about seven days, after which the cocoon is spun prior to pupation. During the wandering period the insect is thigmotactic, so that the cocoons are usually spun in crevices.

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* This study was made in London early in 1947.

The parasite, *Nemeritis canescens*, is parthenogenetic, males being very rare and apparently functionless. It is able to oviposit almost immediately after emergence. Both larvae and pupae are parasitized, and after killing its host, pupation takes place within the host cocoon. The literature on *Nemeritis* is quoted at intervals in the text.

III. STIMULATORY FACTORS.

1. *Smell and Taste.*

The chemical senses residing in the antennae are of primary importance, for it is these which enable the parasite to recognize the presence of its hosts.

(a) *The nature of the response.*

The impulse which brings *Nemeritis* into the vicinity of its host population has been studied by Stein-Beling (1934). Unlike many parasitic hymenoptera, *Nemeritis* does not feed upon the host after stinging; instead, it sometimes leaves the host population if this is possible, and seeks sugary substances, such as nectar. This it generally does immediately after emergence. Using marked individuals, Stein-Beling found that their return was enabled by a sense of smell. The attractive odour is emitted by the host, its silk, and everything it has contaminated. Thorpe and Jones (1937) found that even clean oatmeal, which is a common food of *E. kühniella*, has an odour which is slightly attractive to *Nemeritis*.

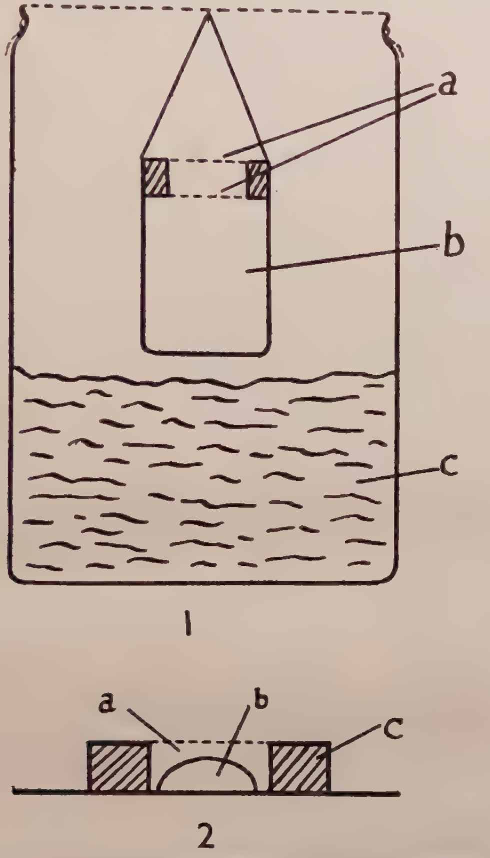
The behaviour of the parasite when in the immediate vicinity of a host has been previously described by Beling (1932), and briefly by Thorpe and Jones (1937). The antennae vibrate rapidly and occasionally touch the substratum, as the insect moves quickly about. When antennal contact is made with a wandering host, or with "traces" of a host (i.e. anything which is contaminated by previous contact with a host), the nature of the parasite's activity at once changes. The scurrying to and fro ceases, the antennae stop vibrating and their tips curl downwards, tentatively investigating the region of host contamination. The stinging valves of the ovipositor are then unsheathed and the region is subjected to a series of tentative jabs.

(b) *Interaction and distinction.*

To this stage *Nemeritis* has displayed two distinct seeking reactions, the first that of a search for "traces" and the second a localized search with the probing ovipositor, both of which are the result of chemical stimulation via the antennae. The response which follows antennal contact with host traces has also been observed with *Habrobracon juglandis* Ashmead (= *Microbracon hebetor* Say) by Murr (Danielczick) (1930), who gave to it the term "Kontakt-Geruchsinn."

The distinction of the two reactions indicates the presence of two primary stimuli, namely those of smell and taste respectively. The physiological distinction of these is difficult to define, but mechanically smell is chemical perception at a distance, and taste is the detection of chemical contact. With *Nemeritis* this distinction is apparent to a marked degree, but has not been clearly appreciated.

To clarify the distinction an experiment was performed to determine if odour alone could initiate stabbing. A large hole was bored in the cork of a 3 in. by 1 in. specimen tube and clean muslin fixed over both ends. This tube containing a parasite was suspended, as shown in fig. 1, within a jar containing an *Ephestia* culture in which the caterpillars were about fully grown. In this manner the parasite was subjected to a strong odour of *Ephestia* while being unable to contact any " traces." A different parasite was used for each observation, and they were left in the tube for a period of 15 minutes if no stabbing occurred. Each parasite which so failed to react was offered a caterpillar on removal from the tube, and if it made no attempt to oviposit, which was infrequent, the observation made with that insect was disregarded. The results are given in Table I. It is seen from this table that parasites of different ages were used; this was an alternative to varying the intensity of the odour, which it is clearly impossible to do with accuracy. The ovaries of a freshly emerged parasite contain a large number of eggs which continue to descend into the oviducts even if no oviposition occurs. The oviducts consequently



FIGS. 1–2.—(1) (*a*) Muslin; (*b*) tube for parasite; (*c*) *Ephestia* infested flour. (2) (*a*) Contaminated muslin; (*b*) *Ephestia* tissues; (*c*) circle of cork.

become greatly distended, and with such parasites stabbing is more easily evoked. Thus parasites up to ten days old were used, none having oviposited, and all having been allowed to feed upon split raisins.

TABLE I.—*Reaction of* Nemeritis *to Odour.*

+ Indicates stabbing ; — indicates no stabbing. All observations at room temperature.

Number.	Age of *Nemeritis* in days.										
	0.	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
1	—	—	—	.	+	.	—	+	—	+	—
2	—	+	—	.	—	.	—	.	—	—	—
3	+	—	—	.	.	.	+	.	.	—	.
4	+	.	—	.	.	.	—	.	.	.	.
5	—	.	+	.	.	.	.	.	.	.	.
6	—	.	+	.	.	.	.	.	.	.	.

Normal stabbing when host traces are found is a prolonged and searching affair, lasting for several seconds unless a host is encountered. When a positive reaction was recorded in the above table, the nature of the stabbing response was clearly abnormal, the insect giving only one or two jabs and then resuming its scurrying activity caused by the odour. Evidently then, there are two stimuli involved, and when the culminative one of taste, or detection of traces (Kontact-Geruchsinn) is not available, there is an inability to complete the seeking reaction of stabbing, or else there is an imperfect reaction.

The organs concerned with the above discussed stimuli are located solely in the antennae, for Thorpe and Jones (1937) amputated these organs and found that insects so treated would not react at all to host stimuli although they could fly normally.

2. *The Influence of Crevices and of the Resistance of the Substratum.*

Host larvae can be classified into three groups according to their availability to the parasite.

(*a*) Those buried in the food material.
(*b*) Wandering fully grown larvae.
(*c*) Larvae in cocoons.

It has already been mentioned that the larvae of the second group are thigmotactic.

When a parasite alights on contaminated food material, e.g. flour, it is stimulated to stab and the ovipositor is repeatedly pushed down into the flour. This it will do for a considerable time if no host is encountered. If, however, it alights on a hard contaminated substratum, although stabbing is evoked, the parasite rapidly moves about until a corner or crevice is found which will allow greater extrusion of the ovipositor, and here it will search thoroughly, as it does the flour. The continual tentative jabbing at a resistant substratum may be interpreted as an attempt to find an aperture, or an area which is soft and yielding, and is an obvious correlation with the habits of the host. The discovery and subsequent thorough probing of a crevice with the ovipositor may be due merely to its initial penetration by chance, but it has also been frequently observed that a crevice is first examined by the antennae.

Thus there seem to be two stimuli which lead crevices to be exhaustively searched : that caused by the greater extrusion of the ovipositor, which occurs when one is accidentally penetrated, and that resulting from antennal exploration. The latter, of course, does not occur without the associated chemical stimuli. The tactile organs of the antennae therefore play a role here in host location.

3. *Movement of Host Larvae.*

Thorpe and Jones (1937) could not obtain oviposition with dead hosts, although such hosts were readily stabbed, and these authors suggest that movement of the host upon pricking is the final stimulus resulting in the deposition of the egg. This is queried by Simmonds (1943), since he found that deeply etherized host larvae were readily parasitized.

To clarify the influence of host movement a number of observations was made on the behaviour of *Nemeritis* to heavily etherized hosts. The parasites used were of different ages and the hosts all of the fully grown wandering stage. All observations were at room temperature.

Oviposition with *Nemeritis* may be deemed successful when the ovipositor sticks momentarily in the host integument and when cleaning movements of the ovipositor, legs and antennae are afterwards performed ; also, further interest in the host is lost for a period. The distinction of this behaviour easily enables an egg-laying thrust to be distinguished from a tentative jab. It was found that the normal stabbing reaction resulted with an etherized larva on a contaminated substratum, but that the parasite found difficulty in appreciating the presence of the host. The stabbing at the host was similar to that at the substratum, and the confined space between the host and the substratum was most attractive (see above section). When a normal caterpillar is pricked, it rapidly recoils and in doing so greatly excites the parasite, which pursues its victim, stabbing vigorously until a successful thrust is achieved. This excitation is exhibited if the host is only able to recoil slightly, e.g. after spinning up. When the etherized larva was tied to a length of cotton which was jerked when the ovipositor touched the host, thereby simulating the normal host reaction, the parasite reacted as it does to a normal host, and oviposition quickly resulted.

With these observations in mind the following experiment was performed. An etherized and a normal caterpillar were placed in a 3 in. by 1 in. tube with a parasite ; the number of stabbings at each during one hour was noted, no attention being paid to whether or not it seemed that oviposition had occurred. This was repeated twenty times with fresh hosts and parasites. The host larvae were then retained for a few days for the parasite eggs to hatch, when they were dissected and the parasites counted. The number of parasites per host is the number of egg-laying stabs it received, and in Table II this figure may be compared, for each host, with the number of stabbings to which it was subjected.

If $D =$ the difference between the means and $E_D =$ the standard error of the difference, then D/E_D, from Fisher's table of x, must give a greater value than 2 for significance at the 5 per cent. point.

TABLE II.

Experiment.	Stabbing.		Eggs laid.		Total eggs laid.
	Normal host.	Etherized host.	Normal host.	Etherized host.	
1	3	2	2	1	3
2	3	2	3	1	4
3	5	2	5	2	7
4	5	5	5	2	7
5	3	6	1	1	2
6	3	2	3	1	4
7	4	2	3	1	4
8	0	1	0	0	0
9	3	2	2	2	4
10	3	1	3	1	4
11	1	3	1	3	4
12	4	4	4	4	8
13	3	1	3	1	4
14	7	1	5	0	5
15	2	0	2	0	2
16	4	4	4	2	6
17	1	0	1	0	1
18	8	6	3	0	3
19	2	1	2	0	2
20	1	1	0	1	1
Totals . .	65	46	52	23	75
Means . .	3·25	2·30	2·60	1·15	3·75
S.D. . .	1·97	1·80	1·54	1·10	2·12

For the elicitation of stabbing by normal and etherized hosts—

$$\frac{D}{E_D} = 1{\cdot}59.$$

For the number of eggs laid in normal and etherized hosts—

$$\frac{D}{E_D} = 3{\cdot}42.$$

Thus there is no significant difference in the elicitation of stabbing by a normal and an etherized host, but the number of successful thrusts at each host *is* different, many less being received by the immobile host. These results verify the above observations, and it may be concluded that the movement of the host upon being pricked is a stimulus of primary importance for oviposition. Furthermore, the ovipositor registers this movement, for when hosts are buried in their food, or are in cocoons, only this organ contacts them. There is no evidence, however, that host movement is always necessary for oviposition or that it is the final stimulus for the deposition of the egg.

4. *Texture of the Host Cocoon.*

Physiologically the host cocoon can be influential in two ways. The first, and established influence which it exerts, is the chemical one possessed by all *Ephestia* silk and contaminated objects. Its other property which is probably stimulatory is that of its texture, for Thorpe and Jones (1937) were able to excite a tentative stabbing at cocoons of *Meliphora grisella* F. with parasites which had been kept for a long period without a chance of oviposition. Such a response must necessarily have been due to the texture of the cocoon, since the normal host chemical stimulation was absent.

5. *Embedding of the Ovipositor.*

The presence along the length of the ovipositor of structures resembling campaniform sensillae was first noticed by Simmonds (1943), and related to their presence is whether the stresses along the ovipositor, caused by its insertion into the host, form one of the stimuli resulting in the deposition of the egg.

A mush of living host tissue was obtained by slitting open larvae and scraping the tissues from the integument. Blobs of the tissue were offered to *Nemeritis*, and its behaviour watched for five minutes, after which time the blood begins to coagulate. Unlike *Pimpla instigator* F., which Picard (1922) found could be stimulated to perform piercing actions with its ovipositor by the blood of its host, *Pieris brassicae* L., *Nemeritis* did not react. Accordingly, the blobs were covered with contaminated muslin as shown in fig. 2. Stabbing through the muslin resulted, but oviposition did not occur.

6. *Physiological Condition of the Host.*

Simmonds (1943) has shown that *Nemeritis* distributes its eggs in such a way that superparasitism is less intense than would be expected if the eggs were distributed entirely at random. This means that *Nemeritis* is able to perceive the internal condition of its host. The work of this author shows that there is no apparent discrimination between parasitized and unparasitized hosts before stabbing occurs, so that the ovipositor is presumably the sensitive organ. This is supported by the work of Dethier (1947), who demonstrated the chemical sensitivity of the unsheathed ovipositor ; furthermore, the only other known method whereby a hymenopterous insect exerts such discrimination is by sensing the previous presence of a parasite, and Thorpe (1938) has shown *Nemeritis* to be slightly attracted, not repelled, by the odour of its own kind.

IV. MECHANICAL FACTORS.

1. *Size of Host.*

Since *Nemeritis* will parasitize caterpillars which are buried in their food material, it is to be expected that the parasite shows no sensory discrimination between hosts of different sizes, even when able to do so by antennal examination. This was borne out by experiment, all host instars were liable to attack when removed from their webs in the food material and presented to a parasite. Oviposition occurred even with first instar larvae, which were so small that they would stick to the sting after being attacked.

The mechanical difficulty of oviposition in small hosts is, however, very great, even when they are placed on a clean substratum, owing to the final trial and error method of location by the ovipositor. This difficulty is even more pronounced under natural conditions, where the young host stages are buried in their food. Since their discovery in such circumstances depends entirely upon chance encounter by the ovipositor, it follows that parasitism of small, early instar hosts is very low. In fact, Voinovskaya-Kriger (1927) and Candura (1928) state that it never occurs; this must be attributed to the mechanical difficulty involved in their location.

2. *The Pupal Integument.*

That parasitism of young *Ephestia* pupae occurs has been stated by Daviault (1930), Arkhangel'skii (1931) and Ahmad (1936). The writer, however, found difficulty in obtaining pupal parasitism. A parasite was placed in two jars, each containing ten young pupae within their cocoons, but no parasitism occurred. Also five larvae, about to spin up, were placed separately in 5 in. by 1 in. tubes, and when they pupated a parasite was added to each, but again no parasitism resulted. Direct observations were then made and the behaviour was seen to be essentially similar to that shown with anaesthetized larvae, the ovipositor exploring the crevices formed by the pupae and the substratum, and paying little attention to the hosts. Several observations were made and only once did oviposition occur.

Evidently the immobility and resistance of the pupal integument is a deterrent to oviposition. The integument of a young pupa cannot offer much resistance to a determined thrust, but its immobility and consequent lack of response when pricked seldom stimulates the parasite to such an action.

V. FACTORS INFLUENTIAL THROUGH METABOLISM.

There are two examples in the literature which serve to illustrate the indirect importance to oviposition of ecological influences which affect general activity.

Feeding upon sugary liquids prolongs the life of *Nemeritis* (Candura, 1928; Diamond, 1929; Daviault, 1930; Beling, 1932; Ahmad, 1936). The total number of eggs laid, however, is unaffected, but the duration of the egg-laying period is prolonged (Ahmad, 1936). It was shown by Stein-Beling (1934) that such feeding will occur after emergence if the parasite has opportunity to escape from its indoor habitat.

Oviposition is independent of the visual sense, since it will occur in the dark; but when parasites are subjected to normal variations of light and dark, and have not been separated from their hosts, oviposition is confined to the period of light (Simmonds, 1943).

The important point emerging from the above is that sugar feeding and light, both factors entirely dissociated from the host, affect the parasite's capacity to react to host stimuli. Periods of insensitivity to these stimuli are lengthened by the former and regulated by the latter.

VI. Discussion and Summary.

The influence of the above discussed factors upon the oviposition of *Nemeritis* may be summarized by forming a composite picture of the parasite's response to them.

To begin, the parasite is attracted to the vicinity of its hosts by their odour, and by the odour of objects or materials which they have contaminated by contact. The food material of the host may also possess an odour which is slightly attractive. The excitation caused by intense host odour causes the parasite to alight and search for regions of host contamination, which, when encountered, stimulate the unsheathing of the ovipositor and a localized probing or jabbing action. The ability of the insect to respond to this chemical stimulation depends upon its feeding, which prolongs the insensitive periods between successive ovipositions ; upon the variations of day and night, if the host habitat is subjected to such light variations, so that oviposition is restricted to the day ; and upon the time which has elapsed since the previous oviposition, for there is a short period of insensitivity following the deposition of an egg. Conversely, if the parasite has been unable to find a host for some time, response is more easily evoked, for the oviducts will then be distended with mature eggs. Response to the host stimuli has so far been effected through the chemosensitive organs in the antennae, which now cease to play any further obvious role.

Contact of the ovipositor with a host is entirely by chance if it is buried in its food material, but if not, then the antennal sense of touch assists by enabling the insect to appreciate crevices and probably also the texture of the cocoon silk. The greater extrusion of the ovipositor which is enabled by a crevice may in itself be a stimulus for its thorough probing. The recoil of a host when pricked so excites the parasite that it performs frantic thrusts with the ovipositor, thereby increasing its chance of penetrating the host's integument. The immobility of the pupal integument is thus an adverse factor for parasitism.

The final stimulus which results in the deposition of the egg is not clear. If the pierced host is already parasitized, *Nemeritis* may refrain from superparasitism by its appreciation of the previous parasitism. This power of discrimination is, however, poorly developed (Simmonds, 1943). The chemosensitivity of the ovipositor established by Dethier (1947) may be effective in this respect, but in the positive sense, that is, in the ability of this organ to detect the interior of the host as a favourable site for the egg and so effect its release, there is only negative evidence, for (*a*) oviposition will result if larvae of *Nygmia phaerorrhoea* Don. are wrapped in the webs of *Ephestia* (Mayer, 1934) ; (*b*) oviposition will similarly occur with larvae of *Meliphora grisella* F. when contaminated with *Ephestia* odour (Thorpe and Jones, 1937) ; (*c*) its own pupae are often parasitized when they are within *Ephestia* cocoons (Narayanan, 1939) ; (*d*) eggs are laid in its own kind by defensive stabbing (Thorpe and Jones, 1937) ; and (*e*) the parasite will not oviposit in fresh, macerated, host tissue. The latter, of course, cannot be described as a favourable site for the development of the egg, but the significant point is that an egg is not released when the ovipositor contacts such naked tissue. The available evidence thus suggests that once the ovipositor has made a penetration which has met with resistance an egg is released, although there may sometimes be a weak appreciation of an adverse host habitat.

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SOME FACTORS AFFECTING THE POPULATION DENSITY AND FLIGHT RANGE OF INSECTS.

By D. S. KETTLE, M.Sc.(Lond.).

THE distribution of insects from their breeding grounds is of great practical importance to public health workers, especially in the tropics, because it is realized that, other factors being equal, the rate of transmission of an insect-borne disease is directly proportional to the density of the vector species, which, in turn, is related to the proximity of the breeding grounds. Therefore before inaugurating any control scheme it becomes essential to obtain an estimate of the distance the vector can fly. It is usual to designate these investigations as studies on the "flight range" of the species. This is an inappropriate term because the variable usually measured is the "population density" of the species and not its "flight range," i.e., the mean distance flown by individuals of the species. Moreover the relationship between these two variables is not constant.

One source of error in population density studies is to neglect the interval between the time of emergence of the adults at the breeding place and their appearance at a given distance from the site. The magnitude of this time lag will depend upon the distance from the breeding site and the rate of outward dispersion of the insect. Therefore if the species shows marked variation in adult production throughout its season, estimations of the population density at different distances from the breeding site at the same time will not be comparable, since each will have been made upon a different fraction of the population. For example, if the average time taken by individuals of a species to reach position A, a yards from the breeding place is α days and to reach position B, b yards away is β days, then if simultaneous estimation of the population density are made on day γ at the breeding site and positions A and B, then these observations are being made on three different populations. The estimation at A is being made on the population which was at the breeding site on day $\gamma - \alpha$, and that B on that which was at the centre on day $\gamma - \beta$. Therefore the most satisfactory estimate of the population is one made by continuous sampling at each position throughout the whole of the insect's season, so that all the estimates are made on the entire population. This consideration will not be so important in areas where the season is long and the population remains more or less static over a relatively long period of time.

In a study of the biting midge *Culicoides impunctatus* Goetghebuer in Scotland a number of catching stations were operated continuously throughout its breeding season. The data obtained provided information on the dispersion of *C. impunctatus* from a small concentrated breeding place. In the present note only the data for male *C. impunctatus* will be considered as the results for the females were almost identical. It was found that the relationship between the insect density and the distance from this restricted breeding site could be expressed satisfactorily in the form—

$$\log. y = \log. a + bx \qquad (1)$$

where y = *C. impunctatus* density at x,
a = ,, ,, at centre of breeding,
b = regression coefficient,
and x = distance in yards from the centre of breeding.

PROC. R. ENT. SOC. LOND. (A) 26. PTS. 4–6. (JUNE 1951).

The decrease in density is brought about by two independent processes. As the midges disperse outwards from the breeding site they become spread over an ever increasingly large area (the " dilution " effect). At the same time the population is reduced by death (the " mortality " effect). The effect of " dilution " on a population can be accurately calculated, and after this has been eliminated the difference between the expected and observed population densities is attributed to the " mortality " effect (fig. 1). This is a general term, since it is not certain what other effects, if any, it incorporates. However, it was found that the " mortality " effect, as defined here, was distributed normally about the mean logarithm of the distance from the breeding site. That is, there is a linear relationship between the percentage " mortality " expressed as probits and $\log_{10}$ of the distance. The full data from which the above conclusions have been drawn will be published elsewhere (Kettle, *in press*).

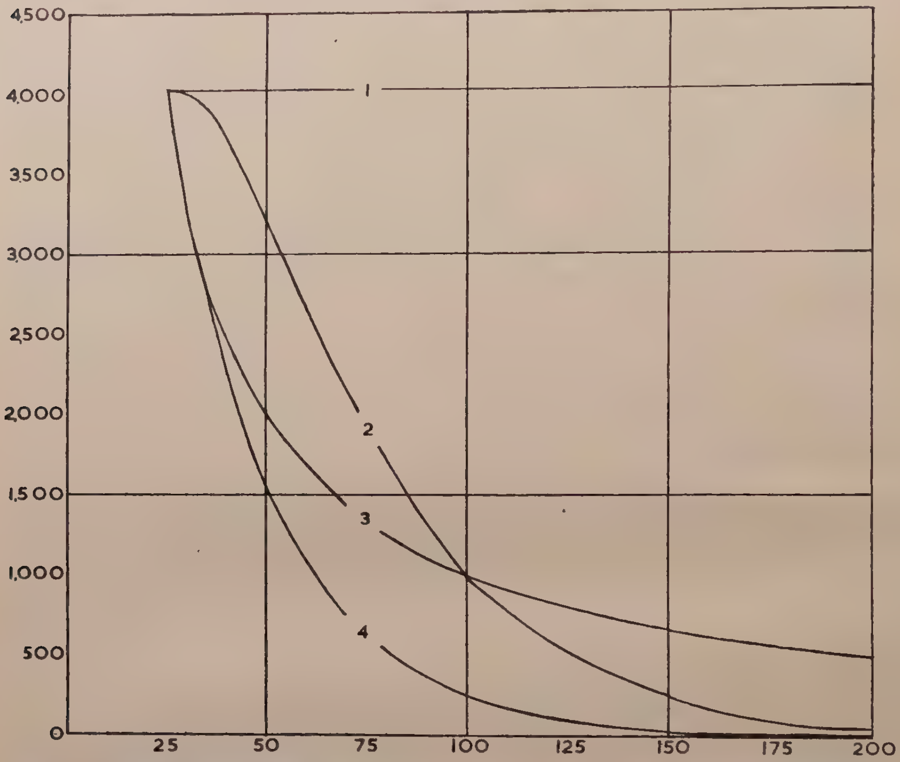

Fig. 1.—Effect of dilution and " mortality " on a population of male *Culicoides impunctatus.* (1) Neither mortality nor dilution at work. (2) Mortality effect alone. (3) Dilution effect alone. (4) Both mortality and dilution effects at work. Ordinate-population density. Abscissa-distance from breeding centre in yards.

These results were obtained from a study of the dispersal of *C. impunctatus* from a small relatively isolated breeding place. Such situations are much beloved by entomologists seeking information about the " flight range " of insects, but are conclusions drawn from such studies of general application ?

Even if the biological conditions remain unaltered will the regression of population density on distance be the same from a small restricted breeding site as from a more extensive one ?

For the purpose of calculation it was assumed that (i) on an unrestricted breeding site the breeding centres were arranged at 10-yard intervals ; (ii) a restricted breeding site had only one centre ; (iii) each centre had position but no size, so that the restricted site was reduced to a point and the unrestricted site to a dotted line ; (iv) each centre produced the same number of adults ; and (v) after emerging the insects dispersed outwards at random so that equal numbers set out in all directions. At any point opposite a restricted breeding site the population is composed of those that set out from the single breeding centre less the losses due to dilution and " mortality." Opposite an unrestricted breeding site the population is made up of many fractions which have come varying distances (x_0, x_1, x_2 . . . x_n), and have therefore suffered various mortalities (fig. 2). The highest contribution will come from the nearest breeding centre, B_0, whilst smaller contributions will be received from B_1, B_1*, B_2, B_2* . . . B_n, B_n*, where B_1 and B_1* are a pair of sites equidistant from B_0, but in opposite directions (see fig. 2).

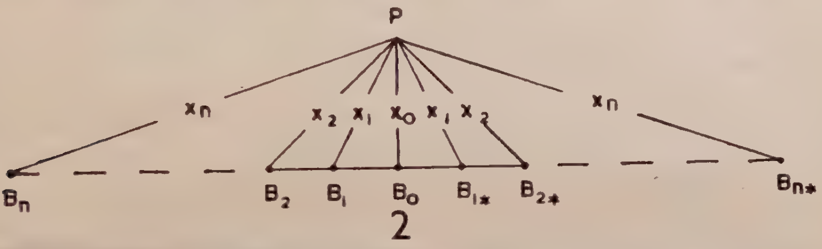

FIG. 2.—Sources of population at position *P* opposite an unrestricted breeding site.

The value of these contributions has been calculated from the data obtained from a single restricted breeding site. The totals have then been adjusted so that the population density 25 yards from the breeding place is the same for both a restricted and an unrestricted breeding site. It will be seen in fig. 3 that the regression of population density on distance is less from an unrestricted breeding site (fig. 3 curve I ; $b = -0{\cdot}0138$) than from a restricted site (fig. 3 curve II ; $b = -0{\cdot}0160$).

In this particular example at relatively great distances from the breeding site, i.e., 1·5 times the average flight range (= 1·5 × 80 yards), the population density from an unrestricted site is about twice that from a restricted site (Table I). Very little difference results either from placing the breeding centres at five-yard intervals or by making them continuous in the unrestricted site. The integral in the latter instance was obtained from Simpson's rule.

One further point is of interest. Although there is a linear relationship between the distance from a single centre and the $\log_{10}$ of the population density, and although this is also true for the insect's dispersal from each centre on an an unrestricted breeding site, it cannot represent the relationship between the population density and the distance from an unrestricted breeding site. This is shown in fig. 3 by the fact that whilst line II is straight, line I is curved. Another example of the whole being greater than its constituent

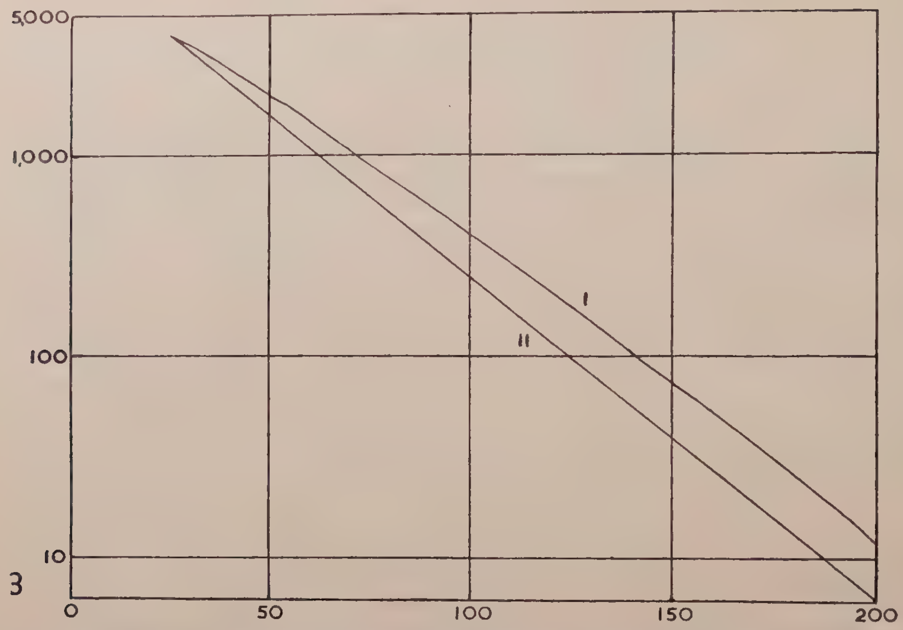

FIG. 3.—Decrease in population density with increasing distance from an unrestricted breeding site (I) and a restricted site (II). Other details as in fig. 1.

parts is found in the phenomenon of growth. Haldane (quoted by Huxley, 1932) has pointed out that if the accurate expressions for the growth of the individual parts of an organ are—

$$\log. y_1 = \log. b_1 + k_1 \log. x,$$
$$\log. y_2 = \log. b_2 + k_2 \log. x, \text{ etc.}$$

where y_1, y_2 etc. = weight or linear measurement of the parts of an organ,
k_1, k_2 etc. = growth coefficients of the parts of an organ,
b_1, b_2 etc. = constants,
and x = weight or linear measurement of the animal,

then the growth of the whole organ will not be accurately represented by

$$\log. y = \log. b + k \log. x \quad . \quad . \quad . \quad . \quad (2)$$

where y, b and k are the statistics for the whole animal. It is interesting to note the similarity between expressions 1 and 2. Both are working approximations to the truth and should be treated as such.

ACKNOWLEDGMENTS

I wish to record my thanks to Professor C. M. Yonge, F.R.S., for granting me the full use of his Department at the University of Glasgow, and to Dr. R. A. Robb and Mr. A. Campbell for their co-operation in working out this problem.

This work was done whilst I was employed as Entomologist to the Sub-Committee on Midge Control, Advisory Committee on Medical Research, Department of Health for Scotland.

TABLE I.—*The Decrease in Population Density with Increasing Distance from a Single Restricted Breeding Site and an Unrestricted Linear Site.*

Distance in yards from breeding site.	(*a*) A single breeding site.	(*b*) Breeding sites in a line, 10 yds apart.	Percentage increase of column *b* over coumn *a*.
25	4027	4027	0
30	3350	3540	6
40	2317	2696	16
50	1603	2017	26
60	1109	1491	34
70	767	1090	42
80	531	801	51
90	367	581	58
100	254	418	65
110	176	301	71
120	122	216	77
130	84	154	83
140	58	110	89
150	40	76	90
160	28	55	96
170	19	38	100
180	13	26	100
190	9·2	18·5	101
200	6·4	13	103

SUMMARY.

This paper is primarily concerned with the relationship between the extent of a breeding place of an insect and the population density/distance regression. It is shown that the population density decreases more rapidly with increasing distance from a small restricted breeding site than from a large unrestricted site even though the initial population densities are the same. This fact becomes particularly important when comparing the results of different workers on the same species.

Attention is also drawn to the misleading use of the term "flight range," since most studies so designated provide no information as to the mean distance flown, but are in fact concerned with the regression of population density on distance.

A further source of error in population density studies is neglect of the time interval between the emergence of the insects at their breeding site and their appearance at a given distance from it.

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OCCURRENCE OF FULLY-WINGED FORMS IN USUALLY BRACHYPTEROUS AFRICAN PYRGOMORPHINAE (ORTHOPTERA.)

By E. Burtt, D.Sc., D.I.C., F.R.E.S.

1. *Zonocerus elegans* (Thunb.).

As stated by Van der Merwe and Kent (1925), *Zonocerus elegans* (Thunb.) occurs in South Africa mainly as a pest on cultivated land. The wings, as a rule, are so reduced in the adult as to be useless for flight, but a small proportion have them fully developed, though such individuals can only fly feebly. The production of the alate form possibly serves to get the species distributed to new localities. Fully winged and brachypterous examples are figured by Uvarov (1928).

Despite seeing brachypterous *Z. elegans* abundantly in Tanganyika Territory between 1935 and 1937, I met with very few alate individuals during that period. In November, 1939, near Morogoro, the fully winged type was more in evidence, and some of the flightless forms exhibited interesting gradations in wing development intermediate between the usual brachypterous and the alate condition. Examples of ordinary brachypterous and of the fully-winged forms of *Z. elegans* are shown in figs. 1–4. Fig. 5 shows an individual in which the wing reduction is intermediate between the other two types. During November, 1942, *Z. elegans* occurred in great abundance in cultivation near Tinde, 26 miles S.W. of Old Shinyanga. Pairs of the brachypterous form *in cop.* were very numerous. Eighty-six alate individuals were found, 63 females and 23 males. Twenty-six of the former and eight of the latter were *in cop.* with the ordinary brachypterous type. *Only two* pairs were seen in which both sexes were of the fully-winged type—indicating that the latter exhibited no special preference for each other. These points are given here so as to enable comparison to be made with observations on *Chrotogonus* given below.

2. *Chrotogonus rendalli* (Kirby).

Members of the genus *Chrotogonus* have a characteristic appearance. Examples are shown in figs. 6–15. They are rather flattened, with a rough integument, broadest across the middle of the body. In my experience the most frequent species is *C. rendalli* (Kirby), or a species practically indistinguishable from it. The lack of reliable diagnostic characters still renders it impossible to know how many species there are. I shall use the name "*C. rendalli*" with inverted commas to include all these similar looking forms. In "*C. rendalli*" (figs. 6, 7 and 8) the wings are vestigial and the elytra are reduced to small scale-like structures, whose dimensions may vary in different individuals of the same sex from the same locality. They occur almost anywhere on patches of bare soil or gravel. I have found it in such diverse areas of Tanganyika as Shinyanga, Tinde, Kahama, Singida, Mkomasi, Amani, Morogoro

PROC. R. ENT. SOC. LOND. (A) 26. PTS. 4–6. (JUNE 1951).

as well as in Swaziland and in the Belgian Congo. In all these areas I have noted the occurrence also of a *Chrotogonus* with well-developed black, fan-shaped hind wings. This form, which is capable of rapid, darting flight, always occurs in relatively small numbers. Examples are shown in figs. 11 and 12. Round Shinyanga and Tinde it appears first in late March and April (late rainy season) and is then more abundant than subsequently; occasional examples, mostly females, continue to occur throughout the dry season and until the rains again break in December. Two, incapable of flight, were taken in which the wings were intermediate in development between this fully-winged form and the ordinary "*C. rendalli*." The one which occurred on 30.iii.45 at Tinde was a male, while the other, on 10.iv.38 at Mpwapwa, was a female. These are shown in figs. 9 and 10. The manner of the occurrence of the fully-winged type and its association with the brachypterous "*C. rendalli*" led me to suspect these were actually two forms of the same species.

On 10.iv.37 I found a pair of *Chrotogonus in cop.* on a gravel road near Old Shinyanga. The male was of the alate type and the female was an ordinary brachypterous "*C. rendalli*." Between late March and early May, 1945, large numbers of "*C. rendalli*" were observed *in cop.* at Tinde. Careful search resulted in 42 pairs being found, in which one of the partners was of the fully-winged type and the other "*C. rendalli*." Of these winged individuals 34 were females and 7 were males. Only two pairs were found in which both sexes were of the fully-winged form. These observations, especially when considered in conjunction with those of *Z. elegans* mentioned above, leave little room for doubt that the black-winged type is the same species as the strongly brachypterous "*C. rendalli*," along with which it occurs.

3. *Chrotogonus* sp.

The validity of the above suggestion with regard to "*C. rendalli*" is supported and strengthened by an analogous observation made in relation to what is obviously quite a different species of *Chrotogonus*. The latter was found abundantly at Mkomasi, in the semi-desert country lying to the east of the Pare Mountains in Tanganyika. All the males were fully winged (fig. 13), and capable of rapid flight. The females (fig. 14) could not fly. They had the elytra fully developed, but the hind wings were reduced. On 21.v.37 a female was taken which could fly, its wings being fully developed as in the males. This specimen is shown in fig. 15. There seems little doubt therefore, that the theme suggested for *C. rendalli* applies also to this other species of *Chrotogonus*.

4. *Tanita dispar* Miller.

In *Tanita dispar* Miller the males can fly but the ordinary females cannot since their wings are too much reduced. Examples are shown in figs. 16 and 17. The degree of reduction in the size of the wings in females may vary somewhat between individuals from the same locality as illustrated in figs. 18 and 19. During late March and April, 1945, *T. dispar* occurred in large numbers at Tinde. Many were *in cop.* Out of about 200 females collected, twelve had the wings developed fully as in the males. Some were observed in flight, and three were *in cop.* with *T. dispar* males. Examples of alate females are shown in figs. 20 and 21.

SUMMARY.

It is a known and accepted fact that *Z. elegans*, which is usually brachypterous, also occurs in a fully-winged form. It appears that this applies also to the three other species mentioned in this paper, *Chrotogonus rendalli* (Kirby), *C.* sp., and *Tanita dispar* Miller. The above account is based entirely on field observations, and serves to emphasize the necessity for systematic work to be linked closely with an adequate field knowledge of the species concerned. The systematist must evidently exercise considerable caution before he attributes specific value to such a character as capability of flight and wing-length in the PYRGOMORPHINAE.

ACKNOWLEDGMENTS.

I am grateful to Dr. B. P. Uvarov, C.M.G., F.R.S., for the interest he has shown in my observations as well as for the advice and help he has given me, and to Mr. F. C. Padley, of the Zoological Department, the University, Reading, for photographing the specimens.

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PLATE 1.

FIGS.

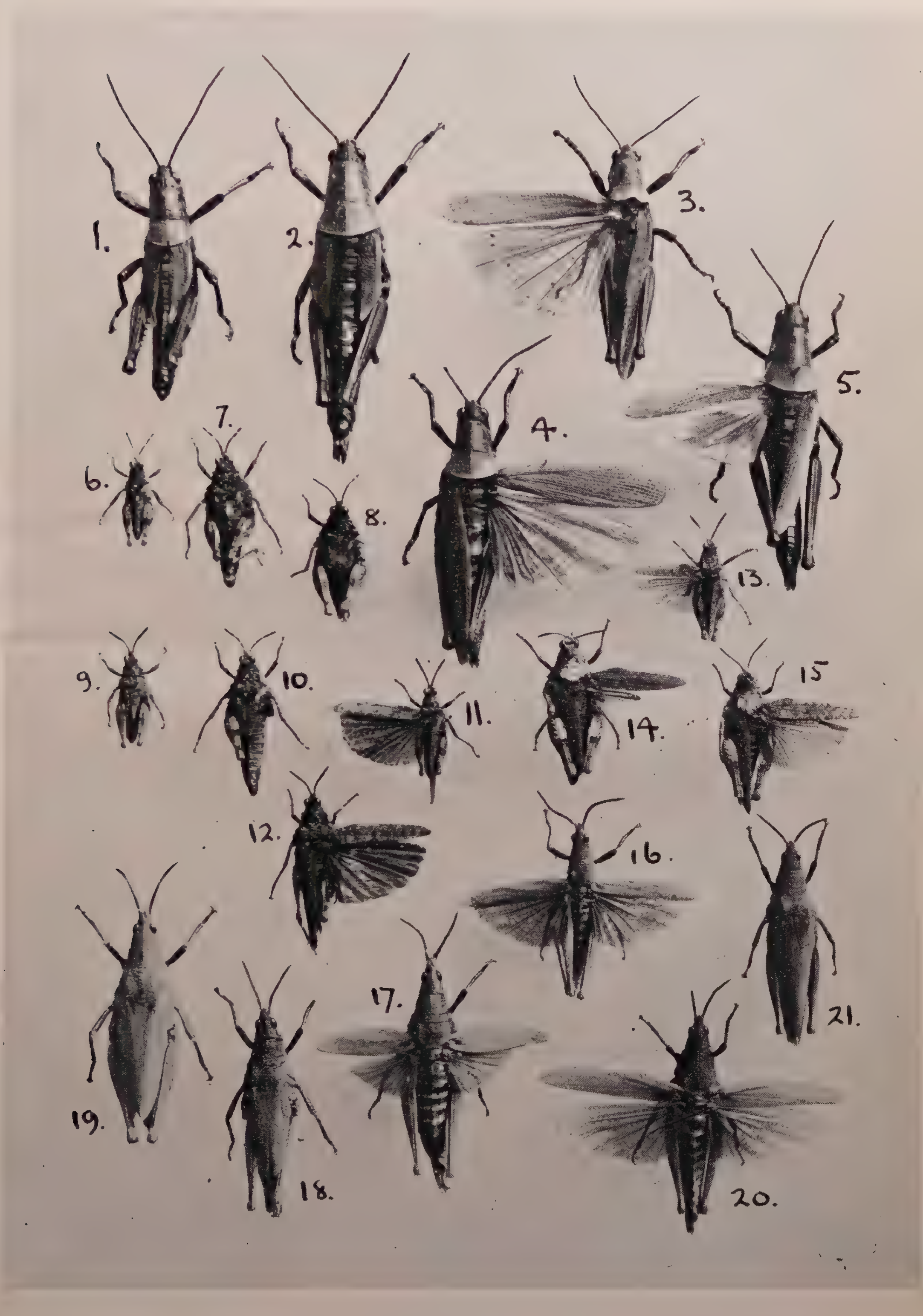
1– 5.—*Zonocerus elegans* (Thunb.). 1. Typical brachypterous male. 2. Typical brachypterous female. 3. Alate male. 4. Alate female. 5. A female showing an intermediate degree of wing development.

6–12.—*Chrotogonus rendalli* (Kirby). 6. Typical brachypterous male. 7. Typical brachypterous female. 8. Female with elytra more developed than in 7. 9 and 10. A male and female with wings more developed. 11 and 12. The alate male and female.

13–15.—Another species of *Chrotogonus*. 13. Male apparently always fully winged in this species. 14. Female. Flightless, but with elytra still well developed. 15. A fully alate female.

16–21.—*Tanita dispar* Miller. 16. Typical male (alate). 17. Typical female (flightless). 18 and 19. Females, the wings of 19 being somewhat more developed than in 17 and 18. 20 and 21. Alate females.

Proc. R. ent. Soc. Lond. (A.) *Vol. 26.* *Plate 1*



African Pyrgomorphinae (Orthoptera)

E. Burtt. Adlard & Son, Ltd., Dorking.

ON A LITTLE-KNOWN PROTECTIVE DEVICE OF SOME CHRYSOMELID PUPAE (COLEOPTERA).

By H. E. Hinton, Ph.D.

(*Department of Zoology, University of Bristol.*)

Some species of butterflies, beetles, and other insects pupate on leaves and exposed surfaces and have no cocoons. These often retain the cuticle of the final instar larva attached to their posterior abdominal segments. Some years ago, while I was investigating the functional significance of this habit, I found that the pupa of a Chrysomelid beetle, *Chrysomela tremula* F., was able when disturbed to expel drops of a poisonous fluid from cuticular reservoirs in the attached larval skin.

I am indebted to Professor G. D. Hale Carpenter for pointing out to me that this was no new discovery but had been recorded long ago by Portschinsky (1890). I am also indebted to Prof. Carpenter for lending me a translation of Portschinsky's paper, a summary of which has been published by Carpenter (1947).

Portschinsky's observations on *C. tremula* F. and *C. cuprea* F. appear never to have been confirmed and are not generally known. For instance, in a recent paper on the biology of *C. tremula* (Bromley, 1947), in which a special section is devoted to discussing the protective devices of the pupa, no mention is made of the remarkable habit with which I am now concerned. I have recently found that the pupa of *Plagiodera versicolora* Laichart. has a similar protective device, and there can be little doubt that at least some other genera of Chrysomelinae will be found in which the larval cuticle functions in the same way.

My observations on *C. tremula* were made on a colony found at Oxshott, Surrey, in the early summer of 1946. The larvae were feeding on a secondary growth of aspen and sallow in an area that had been cleared by fire the previous year.

The mature larva has a large conical tubercle on each side of the last two thoracic and first seven abdominal tergites. In the 1st instar only the glands of the meso- and metathorax are functional, but in the 2nd and following instars functional glands are present on the first seven abdominal segments. These glands are never present on the 8th and 9th segments of the abdomen, as stated by Bromley (1947). When the larva is stimulated, a drop of an odiferous whitish fluid appears on the apex of each tubercle. If it is left undisturbed, the liquid is soon reabsorbed. This liquid is contained in a large reservoir into which open many oval or pyriform, unicellular glands (fig. 1). It is probably salicylaldehyde, which is known to be secreted by homologous glands in the larva of *Chrysomela populi* L. (Claus, 1861), *C. lapponica* L. (Garb, 1915), and another Chrysomelid, *Phyllodecta vitellinae* L. (Wain, 1943), that feeds on willow.

Before they pupate the larvae often wander on to some nearby plant. Here they attach themselves head downwards on a leaf or stem, usually one to three feet above the ground, so that when they pupate the pupa must hang head downwards. The pupa splits the larval skin as far as the metathorax, and then pushes it posteriorly until the first five or six, usually first six, dorsal

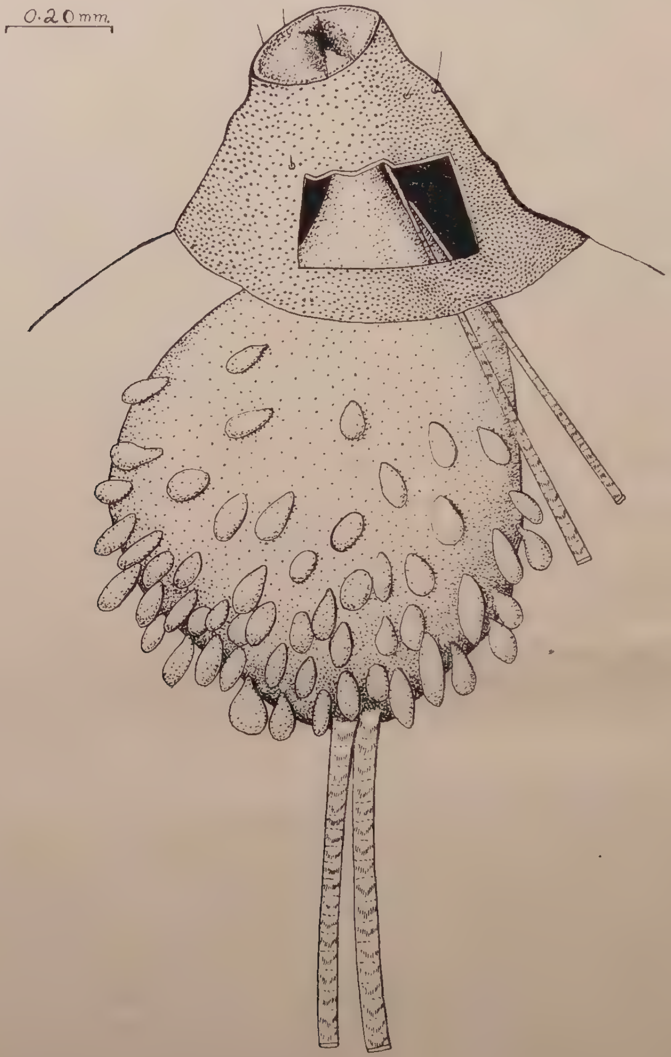


Fig. 1.—*Chrysomela tremula* F. Mesothoracic glands of third instar larva. Some of the pyriform glands have been detached.

abdominal segments are exposed. When the larva moults, the cuticular linings of the reservoirs of the thoracic and abdominal glands are also moulted, and they retain their contents.

When the pupa is stimulated it contracts the dorsal longitudinal muscles of its abdomen so that it jerks upright and its long axis is nearly at right angles to the surface of the leaf or stem. At this time it presses against the larval cuticle so that the fluid in the reservoirs is forced out. This fluid does not spill over, but collects as a large drop on the end of the larval tubercles. When the pupa returns to its resting position, the somewhat elastic cuticle of the reservoirs causes them to regain their shape so that the drop of fluid is sucked in again. In this way it appears that the only fluid lost is that lost by evaporation in the short time that the drop is present at the end of the tubercle, unless, of course, some of it is wiped off on an attacker. The pupal period is usually 5–7 days, and the larval cuticle remains flexible as if covered by an oily secretion. For some time after the emergence of the adult the fluid may be squeezed out of the larval cuticle.

As a rule the response of the pupa to stimulation resulted in the fluid from the thoracic reservoirs being squeezed out, and not infrequently also that of the first abdominal segment. When the pupa responded with unusual violence, a little fluid from the posterior abdominal segments was sometimes also extruded.

The larvae feed together in their first instar. At this time they are dark brown or nearly black, and, as they remain in groups, are very conspicuous. With each moult the cuticle between the dark brown sclerotized plates and the tubercles becomes paler until by the fourth or fifth moult it is dirty white, and the plates and tubercles, now black or nearly so, are very conspicuous as separate spots. At the same time the larvae are less often found together, and shortly before they are mature have become solitary. As others have remarked, this change from a gregarious to a solitary existence coincides with the development of a typical aposematic pattern. Functional defensive glands appear for the first time on the abdomen after the first moult when the larvae are apparently slightly less gregarious, and these glands persist into the solitary phase.

The larval cuticle remaining attached to the pupa is flattened and dilated in an unusual way (for instance compare the pupa and attached larval cuticle of a Coccinellid), with the result that there is no sharp discontinuity between it and the pupa. The pupa is pale yellowish, with black spots so arranged that they enhance the continuity of pupa and larval cuticle. For instance, the knees of the pupa are black and can be seen from above (fig. 2). At first sight they appear to be in the same series as the metathoracic tubercle, whereas the abdominal tubercles of the larva are to an observer perhaps represented by a row of spots on the pupa that is not duplicated on the larval abdomen.

All pupae examined had the 6th dorsal abdominal segment at least partly enveloped by the larval cuticle, and this segment has only two small median dark spots. Segments 7 to 10 are completely covered by the larval cuticle and have no dark spots. The spiracles of the first five abdominal segments are always exposed and functional, whereas the remaining spiracles are covered by the larval cuticle and are functionless. So far as I know, the 8th abdominal spiracles are always functionless in Chrysomelid pupae, so that in this species the retention of the larval cuticle, which is a specialized habit, cannot account for their non-functional condition.

Plagiodera versicolora Laichart. was found feeding on willows on the banks of a river near Keynsham, Somerset, in July, 1950. The pupae are much smaller than those of *C. tremula*, being 3–4 mm. long instead of 8–10 mm.

They were found on the upper surfaces of the leaves. The larval cuticle of this species is also pushed back by the pupa until it conceals only part of the 6th abdominal segment. It is not dilated like that of *C. tremula* and is black or nearly so, whereas the pupa has an aposematic pattern something like that of *C. tremula*. As in the latter species, the glands open at the apices of dorsolateral tubercles on the last two thoracic and first seven abdominal segments.

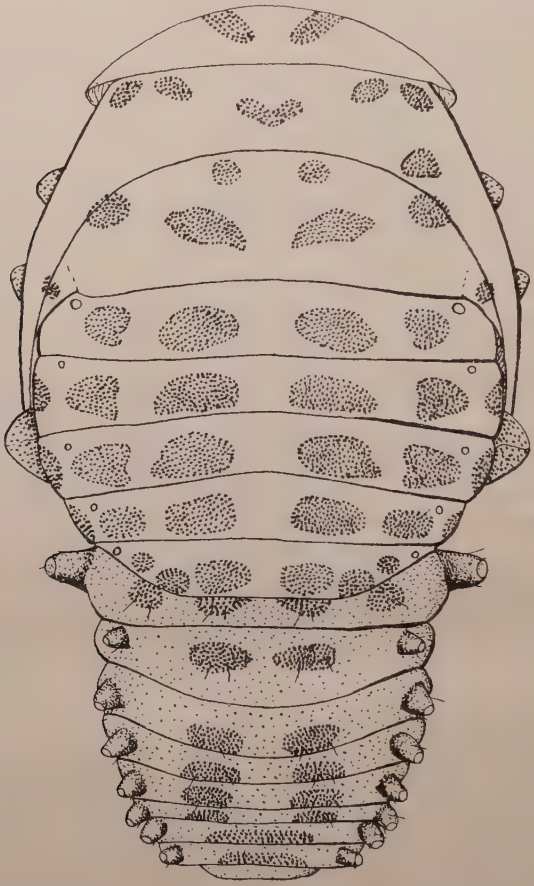


Fig. 2.—*Chrysomela tremula* F. Dorsal view of pupa.

I was not able to find a first instar larva, and do not therefore know if it lacks functional glands on the abdomen. The larvae remain more or less gregarious in later instars, do not develop an aposematic pattern, and do not leave their host plant to pupate.

When the larva moults to pupa, the cuticular linings of the gland reservoirs are also moulted and retain their contents. When the pupa is stimulated and jerks up, it sometimes causes a drop of fluid to appear at the tips of the thoracic tubercles. When it returns to its resting position these drops are sucked in again exactly as in *C. tremula*. Stimulation of the pupa often evokes a succession of rapid jerks. At such times the ventral part of the head is knocked on the leaf and a distinct tapping sound is produced. This sound may of itself have a defensive function, as it is said to have in other pupae, e.g., some LYCAENIDAE.

The spiracles of the first seven abdominal segments of the pupa of *Plagiodera* are functional. Those of the 6th and 7th segments, which are covered by the larval cuticle, are slightly smaller and much less darkly pigmented than the exposed spiracles.

In *C. tremula* the larval cuticle is much more highly adapted to function in defence. That the present habit of pupating in an exposed position and retaining the larval cuticle over the posterior abdominal segments is of some antiquity is indicated by the non-functional condition of the 6th and 7th abdominal spiracles. In *P. versicolora* the fluid contained in the reservoirs is by no means so regularly squeezed out by the movements of the pupa, and pupae were found that did not cause such an emission when stimulated to move. In the latter species neither the outline nor the colour pattern of the larval cuticle and pupa are continuous as in *C. tremula*. These facts, and the still functional spiracles of the 6th and 7th abdominal segments, suggest that both the habit of retaining the larval skin over the 6th and following segments and such protection as may accrue to the pupa from the fluid contained in the larval cuticle are relatively recent as compared with *C. tremula*. Many of the CHRYSOMELINAE pupate in cells in the earth, where the larval cuticle is completely shed, and it seems possible that the pupal habits of *Chrysomela* and *Plagiodera* are independently evolved.

Most endopterygote pupae are concealed in cells or cocoons that afford them some protection against other animals and against adverse changes in their physical environment. Many Lepidoptera, chiefly butterflies, and a few Coleoptera, Hymenoptera and Diptera pupate in exposed places and their pupae are not protected by cocoons of any kind. From a survey of these naked and exposed pupae, it appears that they are in varying degree protected from attack by other animals by possessing one or more of the following:

(1) A hard or spinose cuticle or both.

(2) Procryptic or disruptive colours or tones: These are frequently combined with alterations of shape that subserve the same function.

(3) Aposematic colours: From the little experimental work on pupae that have an aposematic pattern, it appears that all are distasteful to birds, lizards, and other vertebrates likely to attack them. Many of these belong to synaposematic assemblies, i.e., groups of unrelated insects that are found in the same environment, have similar aposematic patterns, and are also distasteful.

(4) Pseudaposematic colours: To this category belong pupae that resemble other animals or plants that because of some attribute evoke an avoiding response in potential attackers, e.g., pupae that resemble the heads of snakes or monkeys.

(5) Distasteful or poisonous fluids: Apparently all pupae that are poisonous also have an aposematic pattern. I know of no pupa that is both procryptic and poisonous.

(6) Sound production: Sound is produced either by knocking a part of

the body against the substrate or by stridulating. This subject has recently been summarized by Hinton (1948).

(7) Gin-traps: Most Coccinellid pupae that I have examined have two or more dorsal median gin-traps on the abdomen. Owing to their size, it is hardly likely that the gin-traps confer any immunity from birds and other vertebrates. That gin-traps can function to repel the attacks of mites and small insects has been confirmed by experiment (Hinton, 1946).

(8) Retention of larval cuticle on posterior abdominal segments: Some pupae do not shed the cuticle of the last instar larva, which thus belongs to a category of cocoons. In many species the last larval cuticle is not entirely shed, but remains attached to one or more of the posterior abdominal segments. This habit is common to many unrelated groups, and it is by no means certain that it has some very general functional significance. It may be present only because pupae stuck to a leaf or twig by some secretion cannot easily shed the last larval cuticle, which may persist if there is not enough selective pressure against its retention. In at least two groups of beetles, however, the persistent larval cuticle subserves a definite but perhaps secondary function:

(A) It may contain a poisonous fluid as in the CHRYSOMELIDAE already described. The pupae of these species have an aposematic pattern. When they are not themselves distasteful, they might be considered to be exceptions to the generalization given in " 3," but then only if considered apart from their attached larval cuticles.

(B) It may have spines that may be thrust against an attacker by appropriate movements of the pupal abdomen. For instance, in *Cassida* (CHRYSOMELIDAE) the two long posterior spinose projections of the larva function in this manner (in addition to carrying the faeces and cuticles of previous instars), and any damage caused to the larval spines by the attacker does not directly injure the pupa. Spines present on the retained larval cuticle may in some cases afford the pupa protection even if they cannot be moved as in *Cassida*.

Effectively to study the full range of structures and habits that subserve a defensive function certain distinctions between the potential attackers must be apprehended. Possible attackers belong to two primary groups: (1) vertebrates that are nearly always very much larger than the pupae; and (2) arachnids and insects that are frequently much smaller than the pupae. For instance, it is fairly certain that of the categories listed above, " 8 " and " 9B " are effective against attackers that are small, i.e., other arthropods. Procryptic, aposematic and other patterns probably rarely confer immunity against other arthropods, and then probably only against some Hymenoptera. In this connection it is interesting to note that very small (1–2 mm.) exposed and naked pupae, that are probably not often eaten by vertebrates because of their small size, are uniformly coloured, e.g., PTILIDAE, CORYLOPHODIDAE, Chalcidoidea. These small naked pupae usually have a relatively harder cuticle than larger pupae, and thus may be protected against many mites and small insects.

I have previously (Hinton, 1946) drawn attention to the fact that pupae concealed in cells or cocoons are not subject to change through selection for procryptic, aposematic, or other colours; and the dull uniform colour of pupae so concealed is in striking contrast to the rich variety of colour found in the exposed and naked pupae of butterflies and beetles. There are exceptions to this rule, but they are the kind of exceptions that prove it. A few Microlepidoptera, GEOMETRIIDAE, and SPHINGIDAE have aposematic patterns but are nevertheless enclosed in cocoons. The cocoons of all such species known to me, however, have an open meshwork through which the enclosed pupa is easily visible, often from some distance.

SUMMARY.

When the pupa of *Chysomela tremula* F. is stimulated, its movements cause the expulsion of a poisonous fluid from the attached cuticle of the last instar larva. The poisonous fluid is contained in the reservoirs of the larval glands and at ecdysis the fluid contained in the cuticle-lined reservoirs is not lost when the larval cuticle is pushed to the posterior end of the pupa. The significance of this habit and the associated structures is discussed. Another Chrysomelid, *Plagiodera versicolora* Laichart., has been found that has a similar habit in a less developed form. A brief summary of the various protective devices of pupae, and the existence of "gin-traps" in the COCCINELLIDAE is recorded.

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PROTHETELY IN *ERNOBIUS MOLLIS* L. (COLEOPTERA: ANOBIIDAE).

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The appearance of pupal or imaginal features in one of the late larval instars of a holometabolous insect is an abnormality which is not uncommon. The most numerous observations of this phenomenon relate to the condition as occurring in the Coleoptera and Lepidoptera and it has been described in a few other orders.

The appearance here recorded of two larvae showing prothetelic characters in a culture of *Ernobius mollis* L. places the Anobiidae for the first time among those families in which the phenomenon has been recorded.

It has been observed by Williams (1914) and others that such abnormal larvae are associated with development under artificial conditions. In most of the cases recorded this appears to be true, for apart from those in which the condition has been experimentally induced, prothetelic larvae have generally appeared unexpectedly among stocks of laboratory reared animals. Prothetelic larvae of the bark-beetle, *Scolytus multistriatus*, have, on the other hand, been found by Beard and Wallace (1941) under natural conditions in elm bark and Kemner (1914) recorded a single case in *Telmatophilus typhae*.

The *Ernobius mollis* larvae referred to, however, were no exception to the general case—the particular culture in which they occurred had been bred under laboratory conditions for two years. At the beginning of July, 1949, seven individuals were removed from this culture for the purpose of studying the prepupa, apparently full grown larvae being selected and isolated in portions of spruce bark.

Of the seven larvae, two pupated normally, two remained as larvae and a fifth died. The sixth larva moulted at the beginning of July shortly after isolation and for one month appeared to be normal; at the end of this time it constructed what appeared to be a pupal chamber in which it lay extended in the characteristic prepupal manner. A faint crescentic pigmentation was to be seen in the region of the future compound eye. This was assumed to portend metamorphosis and accordingly the larva was removed to a cell constructed in cork for the purpose of easy observation. Shortly afterwards the larva moulted but retained its larval form. It was observed to be working actively in the cork. Throughout the following three months the larva appeared normal. It had in the early stages eaten a certain amount of the cork as indicated by the presence of faecal pellets in the frass, but these were absent in the later made galleries which were filled with bore dust only. When next examined, in January, 1950, the larva was found to be prothetelic —the pigmentation of the compound eye was very marked and all the legs were pupal in form. There was no suggestion of wing pads in this individual and all other external features were larval.

The seventh larva was damaged in examination on two occasions; at first soon after it was originally isolated at the beginning of July, 1949, and again in the middle of July. Body fluid exuded in both cases and the larva was expected to die. Instead, however, it soon constructed what appeared to be a pupal chamber in which it remained normal in appearance, although not feeding, until September or October. In October it was found to be prothetelic. Compound eyes were again very obvious; meso- and metathoracic wing pads were present, both pairs well developed. All the legs were pupal in form with the exception of one of the prothoracic legs, which was larval. The third pair of legs possessed double claws as in the imago, while all the rest had single claws as in the larva. The antennae were neither pupal nor larval, being somewhat heavily chitinized and projecting as small cones from the site of the larval antennae. Similar inequalities in the development of the appendages have been recorded in the cases of *Tribolium confusum* (Chapman, 1927; Nagel, 1934), *Monocrepidus lividus* (Thomas, 1933) and *Smerithus* hybr. *hybridus* (Cockayne, 1941). In *Tribolium confusum* and in the longhorn beetle, *Aromia moschata* (Duffy, 1949), an unusual form of the prothetelic larval antenna has also been described.

Although a prothetelic larva may be found to grow rapidly in some cases (Jones, 1883), it is more usual for the phenomenon to accompany a delay in development (Hein, 1920; Pruthi, 1924; Cockayne, 1941). In this connection it is relevant to say that unpublished work by the writer has shown that the speed of development of the larva of *Ernobius mollis* is most readily influenced by the conditions of its environment. At least two years may be taken for the completion of a life-history which can be passed through in rather less than one under apparently more suitable conditions. The reason for the extended period of development is due in most cases to the readiness with which the larvae will pass into a state of partial or complete diapause. To induce this condition, it has often been found sufficient to transplant the larvae into new samples of spruce bark, which, by virtue of differences in texture, nutritive qualities or other unknown factors, act as a check to the growth of the larvae.

The influence of the corpora allata in the control of metamorphosis has been demonstrated by Wigglesworth (1935) in the case of the bug, *Rhodnius prolixus*. The secretion from these glands inhibits the effect of the chemical factors initiating metamorphosis. It has been found by Radtke (1942) that the implantation of larval corpora allata into the abdomen of *Tenebrio molitor* larvae which were due to pupate produced prothetelic individuals in varying degrees of transition from the larval to the pupal state. Further, that the implantation would, if carried out before the last larval moult, inhibit metamorphosis completely, giving rise to an increased size in the larva.

Assuming that the behaviour of the corpus allatum is governed to a certain extent by external conditions, prothetely associated with larvae having an extended developmental period as noted by Hein, Pruthi and Cockayne (loc. cit.), and as described in *Ernobius mollis*, would, under the above construction, not be unexpected. The fact that on most occasions prothetely has been observed in the last larval instar is borne out by the findings of Radtke for

Tenebrio molitor. The same process at work at an earlier stage of larva development would not be recognized as the same phenomenon, since it would then not be apparent externally.

SUMMARY.

Prothetely is described for the first time in ANOBIIDAE, in two larvae of *Ernobius mollis* L. The larvae had been reared under laboratory conditions and had had a protracted period of development.

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